

The Phenetics and Comparative Biology of *Euphilotes enoptes* (Boisduval) (Lycaenidae) from the San Bernardino Mountains

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Abstract. *Euphilotes enoptes* larvae in the San Bernardino mountains utilize both perennial and annual *Eriogonum* species. Many San Bernardino mountain locations have the same *Eriogonum* species; despite this their utilization as hosts varies amongst populations. Seasonal flight periods which correspond to the initiation of the major host's bloom were not only variable amongst populations, but from year to year. One spring emerging population did not fly during 1984 and 1985 and another had shortened flight periods. Despite differences in hostplants and flight periods, these populations appear to be more closely related in larval setation to each other than to six other described subspecies.

Introduction

Populations of *Euphilotes enoptes* (Boisduval) are widely distributed in western North America. They can be found in a variety of habitats from sea level to over 11,000 feet, and from moist cool climates in the Sierra Nevada mountains to the hot dry desert around Palm Springs. The nine described subspecies of this small blue (Miller and Brown, 1981) are often better defined by geographic distribution, flight period, and host plant selection than by adult morphological characters. Distribution of certain subspecies can be quite large as in *E. enoptes ancilla* (Barnes and McDunnough) covering the seven states, (California, Colorado, Idaho, Montana, Nevada, Oregon, and Wyoming) or extremely small as in *E. enoptes smithi* (Mattoni) which is found only along the coast of Monterey Co., California (Shields, 1977). The larvae of *E. enoptes* feed exclusively on blossoms of various *Eriogonum* species. Most subspecies are known to utilize a single host plant species in a given location and all are believed to be univoltine with the flight season coinciding with the onset of the host flowering period. Various populations fly in every month from March to October.

In southern California two subspecies, *E. enoptes dammersi* (Comstock & Henne) and *E. enoptes mojave* (Watson & Comstock) are recognized. The former flies in late summer and fall in the mountains and foothills of the Colorado and eastern Mojave deserts; its larval hosts are *Eriogonum davidsonii* Greene, *E. elongatum* Benth., *E. wrightii nodosum* (Small) Reveal, and *E. w. wrightii* (Torr.) S. Stokes.

Euphilotes e. mojave flies in the spring in the Mojave Desert and western fringe of the Colorado Desert; its larval hosts are the annuals, *E. pusillum* Torr. and *E. reniforme* Torr. & Frem. Shields (1975) speculated on the basis of similarities in distribution and male genitalia that these subspecies are closely related to each other. The life histories of both subspecies have been published (Comstock & Henne, 1965; Comstock, 1966) but the larval descriptions lack sufficient detail to differentiate them from each other or even other lycaenid species. The present study is an effort to better define the ecological and evolutionary relationships of these 2 taxa and to compare them with other named and unnamed montane populations of *E. enoptes*.

The San Bernardino Mts. are an extremely complex and interesting geological area. Here the Mojave and Colorado deserts, the coastal chaparral, and the cooler, moister higher elevations of the mountains all meet. Along the northern and northeastern slopes occur spring flying populations of *E. enoptes*. The northwestern slopes have late summer populations. In the high elevations there are populations that fly in early summer and, depending on rainfall patterns, can be found through mid October. Along the eastern slopes there are populations that fly exclusively in the fall.

Materials and Methods

Studies of *E. enoptes* in the San Bernardino Mountains entailed numerous field observations at four colony sites (figure 1) to determine seasonal activity, host range, and larval behavior. Doble (DB), el. 6700', (2,000 meters) located at the northeastern end of Baldwin Lake, is an open gently sloped flat of rocky clay soil. The major vegetation consists of short ground cover perennials with scattered *Pinus monophylla* Torr. & Frem. and *Artemisia tridentata* Nutt. A second locality (AC) about ten miles (16 km) south-southeast of DB is situated along the steep slope east of Arrastre Creek (AC), el. 7100' (2,200 meters). This site is open with scattered *Juniperus occidentalis* Hook, *P. monophylla*, *Ceanothus cordulatus* Kell, *Cercocarpus ledifolius* Nutt., and a diverse but sparse community of smaller annuals and perennials; the soil is rocky and porous. A third locality about 12 miles west of DB at Big Pines Flat (BP), el. 6800' (2,100 meters), has uneven terrain with *P. monophylla* and *Pinus ponderosa* Dougl. ex P. & C. Lawson forming open stands interspersed with scattered low perennials and annuals. The fourth locality, Mojave River Forks (MR), el. 3100' (950 meters), is 25 miles (40 km) west of DB at the northwestern corner of the San Bernardino Mountains. This site is warmer than the other sites. It is a gently sloped alluvium cut by numerous shallow washes and intermittent creeks; vegetation is diverse, containing elements of Mojave Desert, montane forest, and coastal chaparral communities. Major vegetation includes *Juniperus californica* Carr., *Artemisia tridentata*,



Figure 1. Map of the study sites in the San Bernardino Mts, abbreviations as in the Materials and Methods. Line shows 5,000 ft. elevation of mountains.

and *Quercus wislizenii* A. Dc. with scattered thickets of *Adenostoma fasciculatum* H. & A., *Ceanothus* spp., and *Cercocarpus betuloides* Nutt. ex T. & G. Each of these sites except BP was visited several times during the years 1983 to 1985.

Larvae of *E. enoptes* were also acquired from the following 18 sites (see fig. 2) for comparison of setal characters:

(BG) Bob's Gap, N. base San Gabriel Mts., Los Angeles Co., Ca., el. 4000' (1200 meters), 22. V. 83., on *E. pusillum* GRB; (*E. e. mojave*)

(CC) Chino Canyon, San Jacinto Mountains, Riverside Co., Ca., el. 2600' (800 meters), 27. IX. 83., on *E. davidsonii* and *E. w. nodosum*, GRB & GFP; (Type locality for *E. e. dammersi*)

(CS) Upper Centennial Spring, Coso Range, Inyo Co., el. 6100' (1900 meters), 1. VIII. 83., on *Eriogonum nudum* Dougl. ex Benth., J. F. Emmel; (subspecies undefined)

(EP) El Paso Mountains, vic. Last Chance Canyon, Kern Co. Ca., el. 2500' (760 meters), 19. V. 83., on *E. nudum*, GRB & GFP; (undefined subspecies near *E. e. mojave*)

(LH) Landels Hill Big Creek Reserve, Monterey Co., Ca., el. < 100' (30 meters), 17. VIII. 84., on *Eriogonum parvifolium* Sm. in Reese, GFP; (*E. e. smithi*)

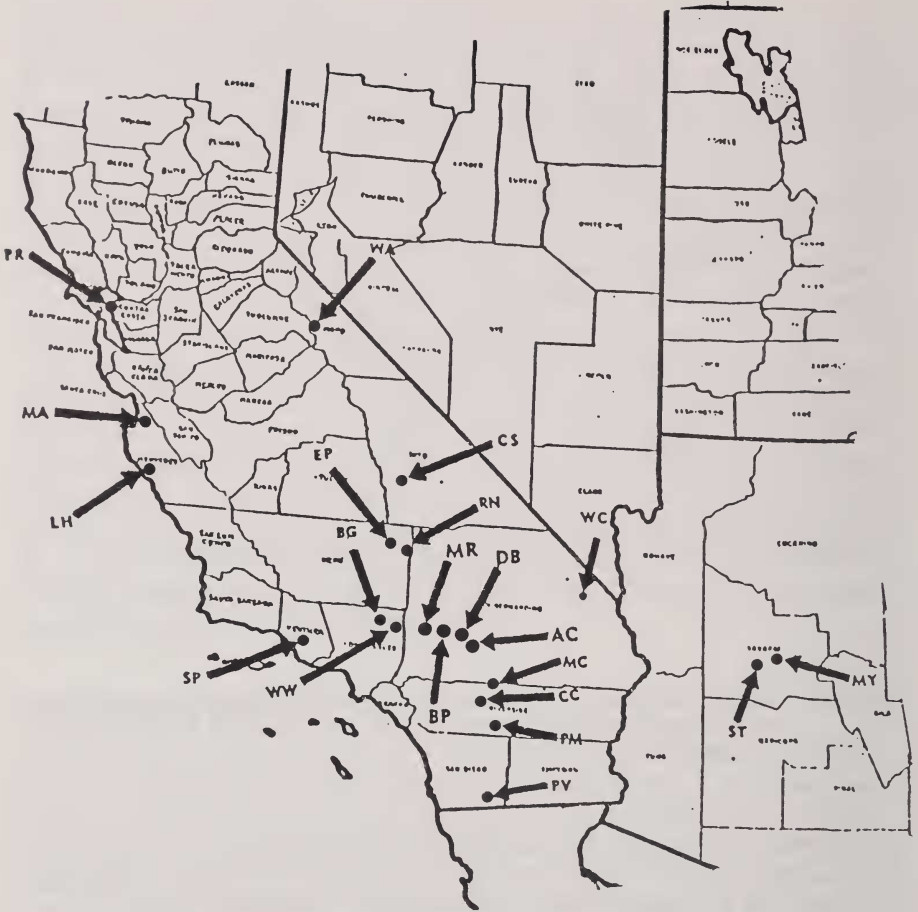


Figure 2. Map of the collection sites; abbreviations as in the Materials and Methods.

(MA) Marina, Monterey Co., Ca., el. < 100' (30 meters), 22. VII. 83. on *Eriogonum latifolium* Sm. in Reese, GRB; (*E. e. smithi*)

(MCA) Big Morongo Canyon, Riverside and San Bernardino Cos., Ca., el. ca 2000' (600 meters), 17. IV. 84., on *E. pusillum*, GFP; (*E. e. mojave*)

(MCS) same data as above except 15. IX. 84., on *Eriogonum elongatum* Benth., GPP; (*E. e. dammersi*)

(MY) Mayer, Yavapai Co., AZ., el. 4500' (1400 meters), 15. X. 82., on *E. w. wrightii*, GRB; (*E. e. dammersi*)

(PM) Pyramid Mountain, San Jacinto Mountains, Riverside Co., Ca., el. 6000' (1800 meters), 17. VI. 82., 6 VI. 83., 1. VII. 83., 26. V. 84., on *E. davidsonii*, GRB & GFP; (subspecies undefined)

(PR) Point Richmond, Contra Costa Co., Ca., el. < 100' (30 meters), 23. VII. 83., on *Eriogonum nudum auriculatum* (Benth.) Tracy ex Jeps., GRB; (*E. e. bayensis*)

(PV) 28 mi. E. of Pine Valley on HWy. 8, San Diego Co., Ca., el. 3500' (1100 meters), 26. VII. 84., on *E. elongatum*, GRB; (*E. e. dammersi*) (RN) Randsburg, Kern Co., Ca., el. 3500' (1100 meters), 19. V. 83., on *E. pusillum*, GRB & GFP; (*E. e. mojave*)

(SP) Santa Paula, Ventura Co., Ca., el. 1000' (300 meters), 20. VI. 84., on *E. parvifolium*, GFP; (*E. e. tildeni*)

(ST) Stanton, Yavapai Co., Az., el. 3500' (1100 meters), 15. X. 82., on *E. w. wrightii*, GRB; (*E. e. dammersi*)

(WA) Warren Canyon, near Tioga Pass, Mono Co., Ca., el. 9000' (2700 meters), 17. VII. 83., on *E. nudum*, GRB & GFP; (*E. e. enoptes*)

(WC) Wildhorse Canyon, Mid Hills, eastern Mojave Desert, San Bernardino Co., CA., el. 4000' (1200 meters), 2. X. 82., on *E. w. wrightii*, GRB & GFP; (*E. e. dammersi*)

(WW) Wrightwood, 1 mi. W., Los Angeles Co., Ca., el. 6000' (1800 meters), 7. IX. 82. and 13. VIII. 83., on *E. nudum saxicola* (Heller) S. Stokes, GRB & GFP; (Shields, 1977, places populations from this area in the nominate subspecies but they may be closer to *E. e. tildeni*)

Larvae were obtained by beating host plant inflorescences, searching for floral shelters, or by rearing from ova. Ova and larvae were often found with other lycaenid species including *Celastrina argiolus* (Linnaeus), *Hemiargus ceraunus gyas* (W. H. Edwards), *Icaricia acmon* (Westwood & Hewitson), *Icaricia neurona* (Skinner), and *Strymon melinus* Hubner. Ova of *E. enoptes* were easily distinguished by their poorly defined chorionic ridges, and larvae were separated by setal outlines. Although color can be variable, larvae of *E. enoptes* are usually yellow or white (never green) with pink or red chevron markings while larvae of the other species are often green. Samples of larvae from all localities were injected with Kahle's fluid, fixed in hot water, and stored in 80% ethanol.

Often larvae were reared on host plants from their collection sites; occasionally, other hosts were substituted. Since *E. enoptes* larvae are cannibalistic they were reared individually in screened vials with flower stalks placed in water to maintain freshness; flowers were frequently changed to avoid mold. Most larvae were permitted to pupate in soil or the rearing container. Pupae were kept under a variety of conditions, as shown in Table 1. Eclosion dates were recorded.

As with most Lycaenids, mature (fourth instar) larvae (Langston and Comstock (1966) and Arnold (1983) state that *E. enoptes bayensis* and *E. e. smithi* respectively have 5 instars, yet in hundreds of rearings of various *E. enoptes* populations we have found only four instars of *E. enoptes*) are covered with short secondary setae and possess a variable number of more prominent (longer and erect) setae grouped in locations where primary setae should occur (sensu Hinton, 1946) (Fig. 3). These locations are dorsal (just lateral to the midline), subdorsal (slightly dorsal to the line of spiracles), and lateral (along the lateral fold). Also, on the prothorax, a few prominent setae occur on the shield

Table 1. Pupae initially kept at 27–35°C were refrigerated (5°C) for at least two months ending in December; afterwards they were kept at 22–27°C. Pupae initially kept at 22–27°C were refrigerated from Dec. 22, 1983 to April 3, 1984 and returned to 22–27°C. Those pupae not refrigerated first year were refrigerated with other pupae their second year for 2–3 months. Those pupae not refrigerated were subjected to moderated daily fluctuations in temperature. The number of pupae from each site is shown in parenthesis.

Pupae kept at 27–35°C	Pupae kept at 22–27°C	Pupae not refrigerated first year	Pupae not refrigerated
AC (4)	BG (5)	MY (1)	BP (5)
EP (7)	BP (9)	ST (1)	MR (3)
LH (25)	CC (3)	WC (3)	DB (54)
McA (15)	DB (8)		SP (3)
McS (65)	EP (8)		MA (1)
PM (7)	MR (5)		
PV (2)	PM (1)		
	PR (9)		
	PV (6)		
	WA (2)		
	WW (3)		

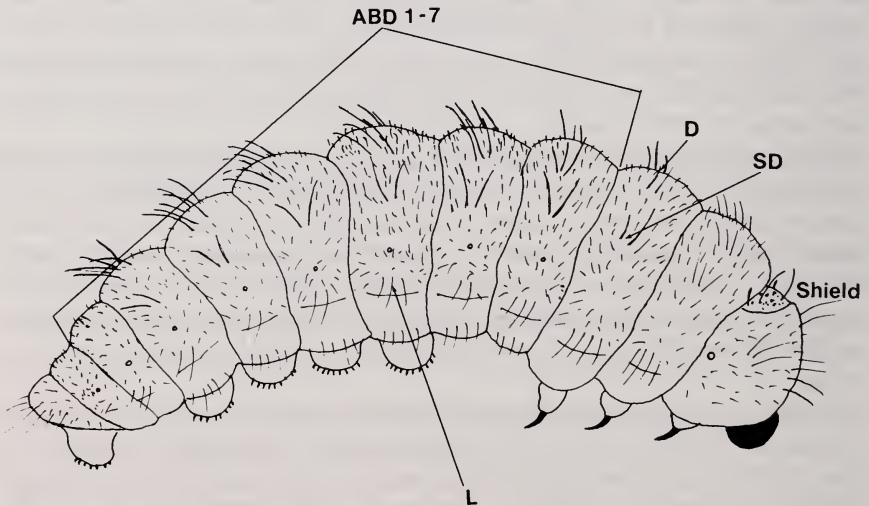


Figure 3. Diagram of an *E. enoptes mojave* larva showing the positions of the setae counted for the 11 characters. Those positions are (D) Dorsal, (SD) Subdorsal, (L) Lateral, (ABD 1–7) Abdominal Segments 1 to 7, and (Shield) Prothoracic Shield.

and many more are located in front of the shield and ventrolateral to the shield in poorly defined groups. Elsewhere, prominent setae occur in specified locations and are most abundant on the mesothorax. No apparent difference in number of prominent setae was found among abdominal segments 1–6 but an increase in number of lateral prominent setae was often noted on the remaining segments. No prominent dorsal setae occur on the seventh abdominal segment in the region of Newcomer's organ (honey gland); also none occur on the more posterior segments.

Both the number and size of prominent setae vary. For comparative purposes the total prominent setae in each location (both sides of the larva) were summed for each segment. Prominent setae were given a value of one if they were at least twice (>0.2 mm) as long as surrounding secondary setae and one-half if they were 1.5–2 times (0.15–0.2 mm) as long as the secondary setae.

Prominent setae in eleven locations were quantified and subjected to statistical analysis using Duncan's Multiple Range Test. These locations were: (1) prothoracic shield, (2) dorsally on the mesothorax, (3) dorsally on the metathorax, (4) dorsally on abdominal segments 1–6, (5) subdorsally on the mesothorax, (6) subdorsally on the metathorax, (7) subdorsally on abdominal segments 1–6, (8) laterally on the mesothorax, (9) laterally on the metathorax, (10) laterally on abdominal segments 1–6, and (11) laterally on abdominal segment 7. Prominent subdorsal setae on abdominal segment 7 and prominent lateral setae on abdominal segments 8–10 may offer characters for statistical analysis but were not included.

A variable number of larvae were used to represent each population; the minimum number was 6 the maximum 30. Consecutive generations of larvae were sampled at DB in June (DB1) and July (DB2) 1983. Samples were taken from MR in September 1982 (MR1) and October 1983 (MR2). These populations were compared statistically to ascertain the stability of mean character states. For the populations PM and WW, larvae from consecutive generations were pooled.

Tables 2–5 present the results of statistical analysis. Populations are listed according to specified abbreviations followed by the number of larvae (n), character mean, standard error, and results of Duncan's Test at the 1% error level.

Results

Larval setation analysis separates the *E. enoptes* populations studied herein into 4 basic groups. The populations of *E. e. mojave* (MCA, BG, RN) have the largest mean number of prominent setae. The number of prominent setae for these populations is significantly higher than for all other populations in dorsal, subdorsal, and lateral positions. With population EP they also have a significantly higher mean number of prominent setae on the prothoracic shield.

Population EP ranks next in mean number of prominent setae in the same locations. It differs significantly from all other populations in prominent setae dorsally on all segments (Table 2) and laterally on abdominal segments 1–7 (Tables 3 and 5). EP and PM together differ significantly in prominent subdorsal setae on the metathorax (Table 2).

Populations CS, PM, and WA often rank together with means higher than all other populations except those above. They are not significantly different from each other in mean number of prominent dorsal setae on all segments and prominent subdorsal setae on abdominal segments 1–6. PM and WA differ significantly from other populations in prominent lateral setae on abdominal segments 1–6; they differ significantly from each other, but not from CS, in prominent subdorsal setae on the mesothorax and prominent lateral setae on the metathorax. PM and CS differ significantly from each other but not from WA in lateral prominent setae on abdominal segment seven.

There is little overall difference in mean number of prominent setae among the populations AC, DB1, DB2, BP, CC, LH, MA, MR1, MR2, MY, PR, PV, SP, ST, WC, and WW. For all setal characters they either do not differ significantly from each other or form a series of overlapping nonsignificant subsets. Populations DB1 and DB2, which represent consecutive generations in June and July, respectively, differ slightly, but not significantly, for all means, except subdorsal setae on abdominal segments 1–6; these are identical. Populations MR1 and MR2, which represent consecutive generations at MR in 1982 and 1983, respectively, differ slightly but not significantly for all means except prominent dorsal setae on the metathorax and dorsal and subdorsal setae on abdominal segments 1–6; these are identical.

Character means for the San Bernardino Mountains populations, (AC, DB1, DB2, BP, MR1, MR2), generally do not differ significantly. However, the mean number of prominent setae on the prothoracic shield is significantly higher for AC than for DB2 and MR2. Also, DB1 differs significantly from MR1 and BP in mean number of prominent dorsal setae on the mesothorax; it also differs significantly from MR1 in mean number of prominent lateral setae on the metathorax and from both MR1 and MR2 in mean number of prominent lateral setae on abdominal segment seven.

According to field observations (Table 6) there are at least three separable populations of *E. enoptes* in the San Bernardino Mts. The one at AC is single brooded and can be found only in the spring. Another population (BP and MR) occurs as adults during late summer and early fall. At DB *E. enoptes* appears in early spring, but can be found, depending on rainfall, into early fall overlapping the flight periods of the two other populations. The rainfall patterns also affected AC and MR over the three years. The spring of 1983 was wet, whereas both 1984 and 1985 were seasonably dry. This may account for adults

emerging up to 2 weeks earlier at DB and MR, and both larvae and adults at AC absent during 1984 and 1985.

Weekly visits to MR during 1982 and 1983 revealed no *E. enoptes* adults or larvae prior to August 21 except three larvae on *E. pusillum* (29. V. 1982) which had similar setation to *E. e. mojave* larvae from BG, MCA, and RN. Although *E. elongatum* and *E. wrightii trachygonum* normally do not bloom until August, *E. davidsonii* is abundant at MR and blooms from spring to summer. However, the only lycaenid larvae found on *E. davidsonii* at MR were *I. acmon*.

The eclosion dates for pupae from the four San Bernardino Mountain sites correspond to field observations. All pupae from DB failed to diapause. Of four AC pupae, initially kept at 27–35°C, one failed to diapause, while the other 3 eclosed within four weeks after removal from refrigeration in January 1984. Three of five pupae from BP did not diapause at 27–35°C. The remainder were kept at unheated Riverside temperatures from December 1983 until they eclosed in July and August 1984. Nine other BP pupae were kept at 22–27°C, and refrigerated from December 28, 1983 to April 3, 1984. They eclosed from May 30, 1984 to July 27, 1984. Five MR pupae were refrigerated and incubated with those from BP, and eclosed July 9, 1984 to Sept. 2, 1984. Another three MR pupae were not refrigerated but kept at 27°C, as with those from BP, and eclosed mid July to mid August 1984.

All three pupae from MY, one from ST, and five from WC eclosed during September and October 1983. In 1984 (after refrigeration treatment) two more from WC eclosed in July and August; one pupa each from ST and WC still remained in diapause.

A variable number of pupae from most locations eclosed within four weeks when initially kept at 27–35°C. These include those from the San Bernardino Mountains, as noted above, DB (50), EP (2), LH (21), MCA (3), MCS (4), PM (1), SP (3), WA (3), and WC (2). Of the pupae initially kept at 22–27°C only those from PV (6), WA (2), and DB (8), failed to diapause.

Many pupae eclosed within 4–5 weeks after removal from refrigeration in December. These include EP (5), MCA (12), and PM (5); one pupa from PM did not eclose in the winter of 1983 but, after a second season including refrigeration again, eclosed in January 1984.

Larvae of *E. enoptes* were found on five species of *Eriogonum* in the San Bernardino Mountains. *Eriogonum davidsonii* is an annual which begins to bloom in spring and may continue into summer and fall, depending on soil moisture. It is the only apparent host of *E. enoptes* at AC and may be the preferred host at BP, since about twice as many larvae were found on it as on *E. wrightii subscaposum*. This plant is absent from DB. At MR it blooms primarily in spring. *Eriogonum kennedyi*, which occurs in a few isolated sites in the San Bernardino Mountains, begins to bloom in May or June; at DB it bloomed during May and June to September during 1983. In 1984 at DB it bloomed

Table 2. The mean total prominent dorsal setae on the mesothorax, metathorax, and abdominal segments 1 through 6; means followed by the same letter are not significantly different at the 1% level.

Locality	n	meso- thorax			meta- thorax			A 1-6		
		mean	S.E.	1%	mean	S.E.	1%	mean	S.E.	1%
MCA	23	8.04	0.54	A	4.41	0.53	A	19.37	1.37	A
BG	17	7.18	0.51	AB	3.88	0.44	A	19.76	1.20	A
RN	19	6.58	0.43	B	4.21	0.38	A	21.11	1.41	A
EP	18	4.72	0.44	C	1.78	0.35	B	10.33	1.59	B
WA	12	3.42	0.29	D	0.00	0.00	C	0.00	0.00	C
PM	17	3.24	0.39	D	0.42	0.19	C	2.44	0.88	C
CS	14	3.07	0.21	D	0.00	0.00	C	0.00	0.00	C
BL1	23	1.08	0.23	EF	0.09	0.06	C	0.13	0.13	C
SP	6	1.17	0.48	EF	0.00	0.00	C	0.00	0.00	C
WW	18	1.08	0.27	EF	0.00	0.00	C	0.00	0.00	C
PR	26	0.98	0.20	EF	0.00	0.00	C	0.00	0.00	C
BL2	17	0.91	0.26	EF	0.00	0.00	C	0.00	0.00	C
MR2	22	0.57	0.21	EF	0.00	0.00	C	0.00	0.00	C
AC	8	0.21	0.21	F	0.00	0.00	C	0.00	0.00	C
LH	30	0.37	0.13	F	0.00	0.00	C	0.00	0.00	C
CC	7	0.29	0.29	F	0.00	0.00	C	0.00	0.00	C
BPF	14	0.28	0.15	F	0.00	0.00	C	0.00	0.00	C
MY	9	0.22	0.22	F	0.00	0.00	C	0.11	0.11	C
MCS	27	0.20	0.10	F	0.00	0.00	C	0.00	0.00	C
ST	13	0.19	0.05	F	0.00	0.00	C	0.05	0.03	C
WC	21	0.05	0.03	F	0.00	0.00	C	0.00	0.00	C
PV	15	0.03	0.03	F	0.00	0.00	C	0.00	0.00	C
MR1	17	0.03	0.03	F	0.00	0.00	C	0.00	0.00	C
MA	10	0.00	0.00	F	0.00	0.00	C	0.00	0.00	C

Table 3. The mean total prominent sub-dorsal setae on the mesothorax, metathorax, and abdominal segments 1 through 6; means followed by the same letter are not significantly different at the 1% level.

Locality	n	meso- thorax			meta- thorax			abd. seg. 1-6		
		mean	S.E.	1%	mean	S.E.	1%	mean	S.E.	1%
MCA	23	7.80	0.64	A	4.28	0.28	A	12.80	1.69	A
RN	19	7.21	0.41	A	4.74	0.30	A	10.63	1.39	A
BG	17	6.76	0.65	A	4.41	0.41	A	11.47	1.29	A
EP	18	4.67	0.29	B	2.22	0.11	B	1.33	0.62	B
PM	17	4.24	0.32	B	1.88	0.30	B	1.06	0.69	B
CS	14	3.50	0.39	BC	0.75	0.20	C	0.00	0.00	B
WA	12	2.50	0.15	CD	0.08	0.06	C	0.00	0.00	B
DB1	23	2.48	0.24	CD	0.43	0.15	C	0.00	0.00	B
DB2	17	2.29	0.28	CDE	0.32	0.18	C	0.00	0.00	B
AC	8	2.13	0.30	CDE	0.56	0.30	C	0.00	0.00	B
MR2	22	1.80	0.26	DE	0.09	0.09	C	0.00	0.00	B
CC	7	1.79	0.46	DE	0.00	0.00	C	0.00	0.00	B
MY	9	1.78	0.32	DE	0.00	0.00	C	0.00	0.00	B
PV	15	1.77	0.19	DE	0.07	0.07	C	0.00	0.00	B
ST	13	1.69	0.29	DE	0.00	0.00	C	0.00	0.00	B
MR1	17	1.56	0.31	DE	0.00	0.00	C	0.12	0.07	B
LH	30	1.52	0.20	DE	0.00	0.00	C	0.00	0.00	B
MCS	27	1.44	0.21	DE	0.00	0.00	C	0.00	0.00	B
PR	26	1.44	0.14	DE	0.00	0.00	C	0.00	0.00	B
WW	18	1.31	0.19	DE	0.03	0.03	C	0.00	0.00	B
MA	10	1.20	0.29	DE	0.00	0.00	C	0.00	0.00	B
WC	21	1.17	0.19	DE	0.00	0.00	C	0.02	0.02	B
SP	6	1.17	0.65	DE	0.00	0.00	C	0.00	0.00	B
BP	14	0.89	0.27	E	0.00	0.00	C	0.00	0.00	B

Table 4. The mean total prominent lateral setae on the mesothorax, metathorax, and abdominal segments 1 through 6; means followed by the same letter are not significantly different at the 1% level.

Locality	n	meso- thorax			meta- thorax			abd. seg. 1-6		
		mean	S. E.	1%	mean	S. E.	1%	mean	S. E.	1%
WA	12	10.83	0.37	A	6.75	0.37	AB	12.29	1.26	C
LH	30	10.05	0.42	AB	3.88	0.42	DEF	0.95	0.32	D
MCA	23	9.91	0.64	AB	8.43	0.54	A	43.28	2.95	A
CS	14	9.64	0.39	ABC	5.14	0.31	BC	5.36	1.38	D
EP	18	9.33	0.63	ABCD	6.78	0.46	AB	30.06	2.65	B
RN	19	9.26	0.21	ABCD	7.47	0.39	A	46.53	1.76	A
SP	6	9.00	0.26	ABCDE	4.25	0.60	CDE	0.00	0.00	D
BG	17	8.76	0.28	BCDE	7.35	0.23	A	43.24	1.49	A
MA	10	8.50	0.54	BCDE	4.10	0.55	CDE	0.10	0.10	D
PR	26	8.04	0.30	BCDEF	4.58	0.41	CD	0.73	0.38	D
BP	14	7.79	0.58	CDEF	3.00	0.50	DEFGH	1.46	0.54	D
WW	18	7.50	0.44	DEFG	3.06	0.45	DEFG	0.64	0.30	D
PM	17	7.00	0.33	EFG	5.00	0.33	C	16.71	1.69	C
DB2	17	7.00	0.23	EFG	2.41	0.38	FGHI	0.88	0.46	D
DB1	23	6.96	0.29	EFG	3.07	0.27	DEFG	2.17	0.79	D
MR2	22	6.45	0.42	FGH	1.18	0.42	HIJ	0.05	0.05	D
MR1	22	6.18	0.54	FGH	2.12	0.51	FGHIJ	0.00	0.00	D
AC	8	6.13	0.35	FGH	2.13	0.40	FGHIJ	0.63	0.30	D
MY	9	6.00	0.87	FGH	0.67	0.47	IJ	0.00	0.00	D
CC	7	5.71	0.57	GH	0.29	0.18	J	0.00	0.00	D
PV	15	5.67	0.31	GH	0.90	0.32	IJ	0.07	0.07	D
MCS	27	5.65	0.26	GH	1.69	0.26	GHIJ	0.00	0.00	D
WC	21	4.86	0.48	H	0.43	0.16	J	0.00	0.00	D
ST	13	4.54	0.49	H	0.69	0.26	IJ	0.00	0.00	D

Table 5. The mean total prominent setae on the prothoracic shield and laterally on abdominal segment 7; means followed by the same letter are not significantly different at the 1% level.

Locality	n	setae on shield			setae abd. seg. 7		
		mean	S. E.	1%	mean	S. E.	1%
RN	19	3.47	0.19	A	7.58	0.50	A
BG	17	3.12	0.23	AB	7.41	0.37	A
EP	18	2.72	0.24	AB	5.33	0.54	B
MCA	23	2.48	0.15	B	7.98	0.34	A
PM	17	1.71	0.24	C	3.47	0.42	C
WA	12	1.67	0.22	C	2.58	0.19	CD
WW	18	1.39	0.20	CD	0.67	0.23	EFG
AC	8	1.38	0.38	CD	0.63	0.32	FG
PR	26	1.23	0.17	CDE	1.06	0.17	EFG
CS	14	0.93	0.22	CDEF	1.86	0.23	DE
DB1	23	0.91	0.21	CDEF	1.43	0.18	EF
MA	10	0.70	0.21	DEFG	0.50	0.27	FG
MR1	17	0.68	0.21	DEFG	0.12	0.12	G
BP	14	0.57	0.20	DEFG	0.46	0.19	FG
LH	30	0.53	0.14	EFG	0.97	0.19	EFG
DB2	23	0.53	0.17	EFG	1.06	0.22	EFG
SP	6	0.33	0.33	FG	0.33	0.21	FG
WC	21	0.24	0.10	FG	0.00	0.00	G
MR2	22	0.18	0.08	FG	0.09	0.09	G
CC	7	0.14	0.14	FG	0.29	0.18	FG
MCS	27	0.11	0.06	FG	0.19	0.08	G
PV	15	0.07	0.07	G	0.17	0.09	G
ST	13	0.00	0.00	G	0.00	0.00	G
MY	9	0.00	0.00	G	0.11	0.11	G

Table 6. The weeks of each month on which L — larvae or A — adults were observed at the 4 different San Bernardino Mt. sites.

	MAY		JUNE				JULY				AUGUST				SEPTEMBER				1
	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1
AC: 1983					AA	L	L	L											
BP: 1983																			L
1985																			L
DB: 1983			AL		A					AL	AL								A
1984		AL		AL															
1985	A			AL															
MR: 1983													A		A	AL	AL	L	L
1984															L	L			
1985															A	A	L		

during May and June and again in September after summer rains. *Eriogonum wrightii subscaposum*, which is common and widespread above 5000' in the San Bernardino Mountains, blooms from August to October. This plant is utilized by *E. enoptes* at BP and DB. *Eriogonum wrightii trachygonum*, which is common mostly below 5000', also blooms from August to October. This plant is utilized by *E. enoptes* at MR. *Eriogonum elongatum*, a common species below 5000', especially along the southern slopes of the San Bernardino Mountains, blooms primarily from August to October. It is the major host of *E. enoptes* at MR.

The presence of the aforementioned hosts does not always correspond to the presence of *E. enoptes*. At MR no *E. enoptes* larvae were found on *E. davidsonii*; nor were any found on *E. wrightii* at AC. Both of these plants are common at many sites in the San Bernardino Mountains where *E. enoptes* has not been found. *Eriogonum elongatum* and *E. nudum*, which is utilized by *E. enoptes* in the adjacent San Gabriel Mountains, are widespread and abundant at many sites along the southern slopes of the San Bernardino Mountains yet no populations of *E. enoptes* are known to utilize them there. *Eriogonum umbellatum* Torr., another common species above 6000', is a preferred host for some populations of both *Euphilotes battoides* (Behr) and *E. enoptes*, but is utilized by neither in the San Bernardino Mountains. In fact, *E. enoptes* larvae from MR die when fed the local *E. umbellatum munzii* (Reveal) as do larvae of *E. battoides glaucon* (Edwards) (J. F. Emmel, personal communication), which utilizes another subspecies of *E. umbellatum* in the Sierra Nevada.

Observations of larval behavior were noted for several populations of *E. enoptes*. In the field, larvae from LH, MR, SP, WW, AC, and PM, often tie together dry and partially consumed flowers to create loose shelters within the host inflorescence. At Morongo Canyon (MCS) mostly first and second instar larvae, rather than later instars, as expected, were found on the host *E. elongatum* from September 15 to November 24, 1984. Under laboratory conditions, these larvae matured to third and fourth instars. The larvae fed nocturnally and remained concealed at the base of host plants by day; they made no floral shelters. Field evidence (the lack of mature larvae on blossoms) suggests that larvae from CC and PV may have a similar behavior.

Discussion

Adult eclosion has two determining factors: conditions which terminate diapause, and thermal summation for subsequent development. Pupae which break diapause simultaneously may eclose at different times in the field due to different temperature regimes (in their environments). *Euphilotes enoptes* pupae from some populations break diapause in response to warming after cold treatment, while others may break diapause in response to other conditions, perhaps independent of cold treatment. When reared under the same conditions, early-flying populations eclose soon after the end of refrigeration, independent of the time of year, while late-flying populations do not eclose until several weeks or months later. Both types of diapause occur in the San Bernardino mountains and one population is facultatively multivoltine.

A high temperature regime (27–35°C) during development is more conducive to breaking diapause (or inhibiting its induction) in *E. enoptes* than is a lower temperature regime (22–27°C). This has been shown in other insects as well (Chapman, 1971). Other *E. enoptes* populations (PV and WA), in addition to the Doble population, appear to be at least bivoltine, as indicated by their pupae failing to diapause when kept at 22–27°C.

Conditions which induce diapause in the multivoltine DB population are not known, but probably are related to host plant condition and/or moisture stress. Some *E. enoptes* pupae can also diapause for more than one year. Termination of diapause in these populations may be affected by rainfall patterns, temperature, and/or photoperiod.

Various populations of *E. enoptes* utilize several species of *Eriogonum* in the subgenera *Eucycla* and *Ganysma* (Reveal, 1969). In the San Bernardino Mountains *E. enoptes* utilizes at least four *Eriogonum* species belonging to both subgenera and often more than one in a given locality. However, not all available hosts are utilized nor are the acceptable hosts utilized wherever they occur. Thus, the distribution of *E. enoptes* in this area is largely independent of availability of hosts.

Euphilotes e. mojave may have the most restricted diet of the *E.*

enoptes subspecies. So far it has been found only on *E. pusillum* and *E. reniforme* even at sites where other hosts occur, as at BG where *E. davidsonii* grows along side *E. pusillum*. Larvae of *E. e. mojave* from MCA collected on *E. pusillum*, which would switch to *E. reniforme* in the lab would not feed on *E. davidsonii* or *E. nudum*. Yet larvae of *E. enoptes* from MR2 collected on *E. elongatum* easily switched to *E. davidsonii*, *E. pusillum* and *E. microthecum*.

First and second instar *E. enoptes* remain within host plant inflorescences. Third and fourth instars, from some populations, often create shelters by tying blossoms together with silk, where they remain until mature or until food is depleted. Older larvae of *E. e. dammersi* at Morongo Canyon do not make floral shelters but probably conceal themselves at the plant base by day and feed on blossoms nocturnally, or crepuscularly. Similar behavior may also occur in some other populations of *E. e. dammersi*.

Setation patterns of mature larvae vary among populations of *E. enoptes*. These patterns are relatively constant from generation to generation and offer reliable characters for comparing different populations. Many populations (*E. e. bayensis*, *E. e. dammersi*, *E. e. enoptes*, *E. e. smithi*, and *E. e. Tildeni*) have very few prominent setae. *E. e. enoptes* larvae have few prominent setae dorsally and dorso-laterally, but a relatively large number laterally on all segments. Larvae of *E. e. mojave* have far more prominent setae than the other subspecies in nearly all body regions. This permits them to be readily distinguished from the others.

Larvae of populations of *E. enoptes* in the San Bernardino Mountains more closely resemble setal patterns of *E. e. dammersi* than *E. e. mojave*, both of which occur nearby. At sites where both *E. e. mojave* and another subspecies of *E. enoptes* occur, as at Mojave River Forks and Morongo Canyon, there is no apparent dilution of larval characters in either. Therefore, it seems unlikely that any gene mixing occurs. Of course, in both cases their flight seasons are widely separate.

The similarity in larval setation of the San Bernardino Mountain populations suggests that these are closely related. San Bernardino Mountains populations of *E. enoptes* are more-or-less intermediate in setal characters between the *E. e. dammersi* populations to the east and populations of *E. e. bayensis*, *E. e. smithi*, and *E. e. tildeni* to the west.

General Conclusions

Larval hostplant and setation characters can be utilized to consistently separate certain populations of subspecies of *E. enoptes* from others. Among the other subspecies (at least *E. e. dammersi*, *E. e. smithi*, *E. e. tildeni*, and the San Bernardino Mountains populations) host plant specificity and seasonal flight period are variable from location to

location. The plasticity of these characters may render them unreliable as indicators of subspecific relationships.

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